

THE BIOLOGY OF *ANTHOPHORA* (*MICRANTHOPHORA*) *PERITOMAE* COCKERELL

(HYMENOPTERA: APOIDEA, ANTHOPHORIDAE¹)

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ABSTRACT: The biology of *Anthophora* (*Micranthophora*) *peritomae* Cockerell is described and compared with that of *A. (M.) flexipes* Cresson. Several habits of *A. peritomae* not observed previously within the genus include: salivary material secreted by larvae; cell refurbishment; and use of communal nest entrances.

Two parasitoids (*Zacosmia maculata* (Cresson) and *Anthrax limatulus artemisia* Marston) were found to attack immatures of *A. peritomae*. Observations on the biology of *Z. maculata* are included. The fungus, *Ascosphaera apis* (Maassen ex Claussen) Olive and Spiltoir, which is the causal agent of chalk brood disease of *Apis mellifera* Linnaeus immatures, grew only on feces within cells.

The biology of the *Anthophora* subgenus, *Micranthophora*, has not been studied extensively. Hicks (1934) reported some biological features of *A. (M.) curta* Provancher and was the first to associate the parasitic bee, *Zacosmia maculata* (Cresson), with *A. curta*. Torchio and Youssef (1968) described the biologies of *A. (M.) flexipes* Cresson and *Z. maculata* and the immature stages of *Z. maculata*. This paper describes the biology of *A. (M.) peritomae* Cockerell and makes comparisons with the biology of *A. flexipes*. New observations on the biology of *Z. maculata* are also included.

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HABITAT

Anthophora peritomae was found nesting in an eroded, vertical embankment adjacent to Bear River, two miles east of Cornish, Cache County, Utah, during September and October, 1968. This embankment, formed by sedimentation of the river and subsequent erosion, was composed of coarse-grained, pebble-free, tightly-packed greyish sand. It measured 4.5 m in height and

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18.3 m long, was devoid of plant growth and curved from a south to an east exposure. Dense aggregations of nests (more than 30 per square meter) were found in limited areas between the 0.5 and 2-m levels on the south and southeast slopes which were exposed to the early morning sun. Most entrance holes were shaded from the sun by 2:00 PM Mountain Standard Time (MST). On clear days, flight occurred whenever the temperature rose above 24° C (usually from about 9:30 AM to 6 PM), but little flight took place during cloudy weather though temperatures often rose above 24° C.

NEST ARCHITECTURE

Entrance Hole: The structure, dimensions, and construction of entrance holes were similar to those of *A. flexipes*, which nested in the vertical embankments near Moab, Utah (Torchio & Youssef, 1968). Both species also employed the same method (rapid flicking motions with the hind legs) to remove soil from the nest. *Anthophora peritomae*, however, initiated construction of new nest burrows throughout the daily flight period and directed them into the substrate at various angles. Because nests of *A. flexipes* found near Cornish were constructed in flat or gently sloping sand surfaces, they were surmounted by ellipsoidal tumuli formed by excavated sand flicked backwards from the nest entrances.

Burrows: Burrows constructed by both species were similar: They had the same diameter and their walls were not lined with secreted materials. Also, the lateral burrows were comparable in length, and each was partially plugged a short distance above the cells with loose, dry sand excavated from new burrows or from one or more areas along existing ones. The main burrows and entrance holes remained unplugged during and after nesting activities.

The nesting site of *A. peritomae* was completely honeycombed with nests constructed in previous seasons. As a consequence, even the most careful excavations were inadequate to trace the branches associated with each nest. The problem was compounded when I found that the bees commonly used communal entrances. However, once I devised a method to establish the number of females using a communal entrance, it was possible to decipher the architecture of individual nests branching from the common entrance cavity.

To observe those bees using a communal nest and to distinguish between them, I marked each bee (without disturbing it) in such a way that I could recognize it for several days. Small spots of lacquer or oil-based pigments painted on the mesonotum or apical terga were unsatisfactory: some bees died within minutes after application; others became disoriented; and many quickly removed the markings. In contrast, bees dusted with fluorescent powder were apparently unaffected. This material was applied by blowing a small quantity of powder through a soda straw directly onto a bee hovering

in front of her nest entrance. The powder, which adhered to body hairs, was quite visible on most individuals for at least four days.

Seven communal nests were observed in this study, and each occupant of each nest was marked with a different colored powder. The number of females per nest was small (minimum, three; maximum, six), and the nest architecture was variable. In four nests, a large communal chamber was excavated immediately behind the common entrance hole, and each burrow leading away from it represented an individual nest. Each nest was normally composed of a main burrow and several lateral burrows, each originating at a particular point along the terminal half of the main burrow. The lateral burrows meandered for variable distances until they terminated in cells. The entrances to the communal chambers were normally enlarged gradually during the nesting period. When nesting was completed, they were nearly as wide as the chambers.

A fifth nest lacked a communal chamber, and each burrow originating along the entrance burrow represented an individual's nest which normally possessed its own lateral burrow system. The entrance hole and burrow, however, were not enlarged as one might expect. The other two nests studied were multi-entranced and lacked communal chambers. One of these nests, occupied by four bees, had three entrance holes; the other, which possessed four entrances, housed three bees. These multi-entranced nests were more than likely developed when burrowing bees accidentally broke into existing nest burrows of other solitary nesting bees. Subsequently, these drilled-into burrows became interconnecting, communal nests. Occasionally, burrowing bees would happen onto inactive nests excavated in previous years, whereupon they often, but not always, incorporated them into their nest architecture.

When the entrance of a single-entrance nest containing five females was plugged with cellucotton, each returning bee hovered directly in front of it for a short period. Then she darted about searching the surrounding bank for five to 10 seconds before she returned to her original hovering position. After several minutes, she flew away and then returned a few minutes later to repeat the same pattern. After an hour, one bee landed on the plug and tried to pull it loose. Soon, two others joined her, and the three (sometimes working together and sometimes individually) removed the plug in 3 hr., 52 sec. and re-established communal nesting. The fourth female reoriented to an abandoned nest several meters away, and the fifth bee excavated a new nest 30 m away. A check of the five bees four days later proved that the forced reorientation was permanent.

Bees inhabiting nests with more than one entrance also varied in their behavior. Normally, one entrance hole was entered by two or more bees and the others were each utilized by one bee. These bees continued to enter and exit through the same holes even after the main or a lateral burrow was partially exposed by the burrowing activities of another bee or by my exca-

vations. If an entrance used by one female was plugged while she was in the nest, she quickly located another exit hole, oriented to the new entrance by hovering in front of it for a few seconds, and then flew in a lateral zigzag and figure eight pattern in front of and directly away from it. Subsequently, she used the new entrance exclusively. Conversely, a bee returning to a nest whose entrance was plugged while she was away was unable to locate alternative entrances and abandoned her nest. Those bees utilizing communal entrances associated with multi-entranced nests seemed to be strongly oriented to their entrances. If a communal entrance was plugged while the bees were in the nest, they sometimes drilled another hole as close as possible to the original. At other times, bees escaped from other entrances in the nest but then returned to the blocked entrance and tried to unplug it. If they could not remove the plug, they usually excavated another entrance near the plugged one. However, in one case, two bees abandoned their nests and started new solitary nests 40 and 48 cm distant.

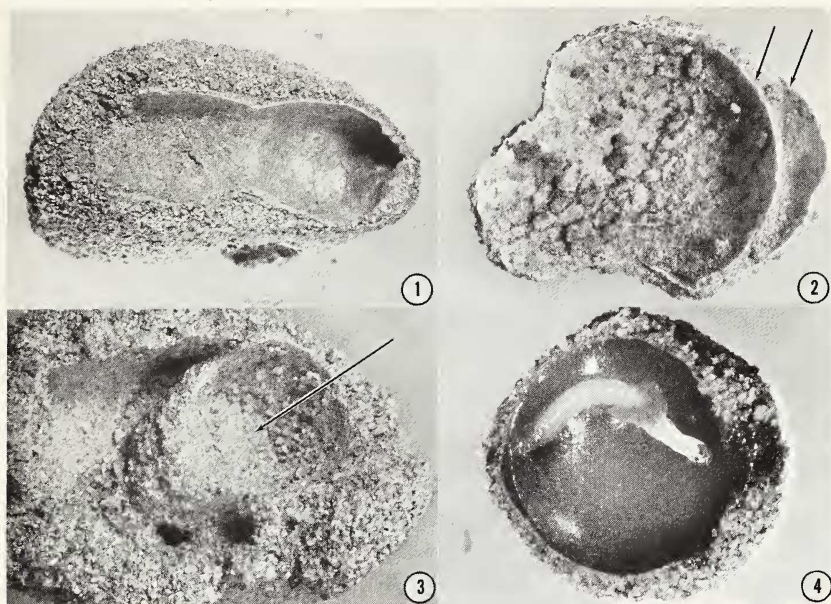
Although plugging the entrances with cellucotton disturbed the orientation of the bees, carving the entrances or applying fluorescent powder did not. Also, careful observations revealed that most nests were occasionally entered by bees from other nests. Some of these visitors deposited one or two loads of pollen. Two such bees, marked as they left the alien nest, were subsequently discovered nesting within a 45 cm radius.

Cells: Cells of *A. peritomae* and *flexipes* were similar in shape, placement at the terminus of burrows, extractability from surrounding soil, attributes of the cell lining, and details of the cell cap. Although both species commonly constructed a single cell at the terminus of each branch burrow, *peritomae* placed two to four cells in linear series or in loose clusters at the terminus of nearly 20 per cent of the burrows studied. Cells in linear series were usually separated from each other by a plug of loose sand 2 to 3 mm deep, but I found one series where cells were joined. Both species placed cells at various declinations ranging from subhorizontal to perpendicular.

The area immediately in front of most cells of *A. peritomae* was hollowed, resembling the basal area of typical cells (Fig. 1). The inner surface of these antechambers was lined with small, uniform soil particles similar to the soil lining found in cells, but it lacked the secreted, waxlike lining characteristic of true cells. Although this antechamber (8 mm long by 6 mm wide) was completed during cell construction, its function was not determined. Antechambers were reduced or lacking in front of cells constructed in linear series.

Cells of *A. peritomae* did not vary in size (10 by 8 mm), shape, or structure. Construction of cells was begun when the terminus of the burrow was carved into a crude cell with dimensions slightly larger than those of the completed cell. The final cell walls were formed by lining the roughed-in cell with small soil particles of a relatively uniform size extracted from other

areas within the nest. The cell was then coated with a thin lining of a transparent, waxlike secretion. Cell cap construction was not observed, but completed caps were lined with a waxlike material and were nearly identical to those constructed by *A. flexipes*.



FIGURES 1-4. *Anthophora peritomae*. Fig. 1. Longitudinal section of cell and unlined antechamber. Fig. 2. Basal area of cell with arrows designating the 2 waxed linings. Fig. 3. Cell constructed across open space. Arrow points to cell cap. Fig. 4. First instar larva nearly free of its egg chorion.

During excavations of *A. peritomae* nests, one cell was found with two wax linings separated by a thin layer of soil (Fig. 2). Thus, *peritomae* refurbishes and relines abandoned cells in some circumstances. This time-saving habit is, surprisingly, not often practiced by bees except for some Apidae and some Megachilidae. Another cell (Fig. 3) was found positioned across the diameter of a burrow, suggesting that the species can construct cells across unsupported spaces.

PROVISIONING AND DEVELOPMENT

Nest provisioning by *A. peritomae* (Fig. 13) was studied from September 5 through September 10, 1968. Similar studies of *A. flexipes* (Fig. 12) were made a few weeks earlier at the nearly flat-surfaced sandy area one mile to the north. *A. peritomae* required an average time of 5 hr, 50 min to provision a cell: this included the deposition of 20 pollen loads in a period of 1 hr, 50 sec (an average of 3 min/load); and a foraging period of 4 hr

(an average of 12 min, 37 sec/trip). *A. flexipes* deposited 18 pollen loads/cell (Fig. 12) in 1 hr, 18 min (an average of 4 min, 20 sec/load); and the foraging period was 1 hr, 27 min, 30 sec (an average of 6 min, 44 sec/trip). Thus, the two species were very similar in their provisioning behavior at Cornish in spite of the dissimilarity in their nesting habitats.

The bottom three-eighths to one-half of each *A. peritomae* cell was filled with a dark yellow, pastelike provision. Samples of pollen taken from 10 cells proved it to be *Grindelia squarrosa* (Pursh) Dunal (determined by G. E. Bohart), which was the predominant flowering species near the nesting site. *Anthophora peritomae*, unlike *A. flexipes*, stored pollen as a nearly dry, asymmetrical ball. When the provision was nearly complete, liquid (probably regurgitated nectar) was added until the mass became a semiliquid that filled the bottom half of the cell. The surface of the completed provision was tacky to the touch, but it was not covered with a layer of nectar. The pungent odor characteristic of anthophorine cells was present in the cells of both species.

The egg of *A. peritomae* was dull white, opaque, weakly arched, and measured 3.5 mm long by 0.9 mm wide. It was deposited on the surface of the provision and was attached to it only by its tips which were slightly embedded (Fig. 5). The egg was always positioned with its narrowed anterior tip (0.5 mm wide) less than 1.0 mm from the cell wall and with its broadened, posterior tip (0.9 mm wide) resting on or near the center of the provision. The position of *A. flexipes* eggs as described by Torchio and Youssef (1968: 292-293) should be reversed: the narrowed, anterior tip of each egg faced the cell wall and the broadened, posterior tip rested near the center of the provision's surface.

The egg was turgid when deposited, and its surface, though minutely reticulated, was slightly reflective. As the embryo matured, this turgidity and reflectivity were gradually lost. The first instar completely freed itself from the egg chorion 68 to 74 hours after the egg was deposited. Emergence was signaled by the splitting of the chorion along the pleural region directly above the spiracular line of the embryo. Within 10 hours, the chorion was completely separated between the anterior and posterior spiracles, and, during the eleventh hour, it split transversely between the anterior pair of spiracles. Also, the posterior areas of the chorion separated rapidly until the four posterior abdominal segments of the first instar larva were exposed. The pleural region of the chorion then separated anteriorly above the prothorax of the larva and finally above the lateral and posterior margins of its head capsule. The first instar was completely freed from its chorion (Fig. 4) within 12 hours after the chorion began to separate from the head capsule. Subsequently, the chorion was represented by two chorionic strips lying on top of each other on the surface of the provision directly behind the larva.

The first instar encircled the outer edge of the provision as it fed (Fig. 8), and it usually completed one circle before molting. The second and third instars followed the same pathway and consumed sufficient quantities of



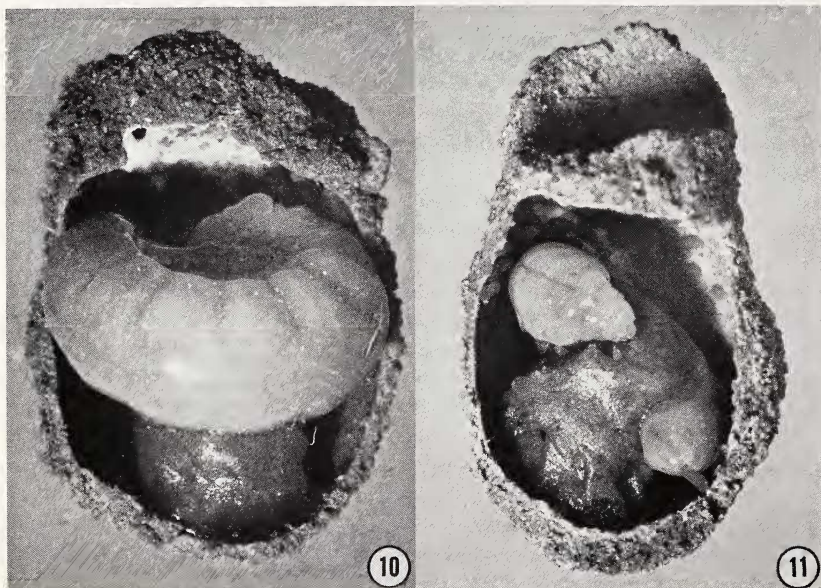
FIGURES 5-9. *Anthophora peritomae*. Fig. 5. Position of egg on provision within cell. Fig. 6. Dissected cell exposing anal excreta smeared on cell wall and partially covered by a few sausage-shaped fecal particles. Fig. 7. Fecal particles with one having a transparent thread extruding from it. Fig. 8. First instar encircling provision as it feeds. Egg chorion visible on central surface of provision. Fig. 9. Last instar forming a cone-shaped provision as it encircles and consumes the outer edges.

pollen to furrow the outer edge of the provision, leaving a central pillar. The last instar enlarged and deepened the furrow as it fed until the provision was shaped into a conelike structure whose sides sloped nearly 60 degrees (Fig. 9). The larva then lifted its posterior abdominal segments until its anus touched the cell wall immediately below the cell cap and deposited a light gray, granular material through its anus. This material, as seen through the translucent cuticle, was stored in a pair of convoluted tubules within the terminal body segment. Each tubule emptied into the colon immediately behind the zone filled with feces. Within 43 minutes, the larva had smeared the material (probably Malpighian excreta) across a limited area adjacent to the cell cap by oscillating its terminal abdominal segment. The thin coating dried rapidly into a brittle scale which remained firmly attached to the cell wall (Fig. 6).

As the feeding larva was completing deposition of the anal excretion, it began to deposit a salivary material as a rapidly drying, shiny, transparent thread. This material was secreted onto the provision continuously for 5 to 9 hours. Eventually, the larva ingested these threads as it consumed its provision. Since it made no attempt to construct a cocoon, the function of the salivary secretion is not understood. Possibly, it serves a nutritive role, or it may merely represent the vestige of a cocoon-spinning habit.

When the larva had voided its anal excreta and salivary secretion, it rapidly consumed the remaining provision by two methods of feeding: most larvae fed upon the surface of the provision until it was consumed; others continued to encircle and deepen the furrow around the outer edge of the provision until it was shaped into a parallel-sided column (Fig. 10). Then the larva consumed the basal area of the column (Fig. 11) until it rested with its terga at the bottom of the cell beneath the provision. Eventually, the head and anus of the C-shaped larva faced the cell cap with the medial abdominal terga resting on the bottom of the cell and the provision resting on the medial abdominal sterna. At this juncture, the subspherical food remnant was rapidly consumed.

Defecation was usually begun about 8 min after the larva deposited its anal excreta. The first fecal particles were deposited adjacent to or covering this layer (Fig. 6). The sausage-shaped fecal pellets measured 0.75 to 1.10



FIGURES 10-11. *Anthophora peritomae*. Fig. 10. Last instar larva encircling the parallel-sided provision shaped by the feeding larva. Fig. 11. Position of last instar larva as it begins to consume basal area of provision. Some fecal particles have been deposited on the cell wall, and one is extruding from the anus of the larva.

mm long and 0.5 mm wide. They were subcylindrical, but both tips were dorsoventrally flattened and blunted apically. Also, each tip was provided with one to three thin, transparent threads which interconnected the pellets. At least one thread was continuous as it traversed the core of the fecal chain.

Several partially extruded fecal particles were gently extracted from the anus of various larvae. In each case, a transparent thread which entered the posterior tip of the fecal particle was also pulled from the anus (Fig. 7). The material resembled a strand of molten glass when it was first exposed to air, but it dried quickly into a brittle, shiny thread. The thread varied in length (9 to 18 mm) and was incorporated into each fecal particle prior to its emission.

Defecation was not continuous. At times, three or four pellets were deposited within a 2-minute period and then an hour or more of inactivity followed before additional pellets were deposited. Defecation was completed approximately three days after it was initiated. *Anthophora peritomae*, unlike *A. flexipes*, deposited unappressed fecal particles on the cell walls, but like *A. flexipes*, it did not normally smear feces over the inner face of the cell cap.

The postdefecating larva of *A. peritomae* quickly changed in appearance: it became semiflaccid; its integument turned an opaque, cream color; and it assumed a nonmotile, C-shaped, overwintering position. Seventy such prepupae collected from the nest site on October 8, 1968, were stored in the laboratory at room temperature (21-24°C). Although none were cold-conditioned, six adults emerged in late December and 24 more emerged by May 1. The remaining 40 larvae were then cold-conditioned throughout the month of May at 5-7°C, and most of these emerged as adults during the third week of June. The sex ratio was 1:1.

In the field, *A. peritomae* overwinters as a prepupa. Pupation occurs during mid-August, and most adults have emerged by September first.

ASSOCIATES

Two parasitoids (a melectine bee, *Zacosmia maculata* (Cresson) and the bombyliid fly, *Anthrax limatulus artemisia* Marston) were reared from cells of *Anthophora peritomae*.

Four planidia of *Anthrax l. artemisia* were recovered from three of several hundred host cells excavated during the nesting season. One active planidium in each of two cells was crawling on the provision adjacent to the host cell. In the third cell, two planidia were found, one crawling over the surface of the provision and the other crawling back and forth on top of the first-instar host larva. Also, on October 13, 1968, 68 host cells were collected from the nest site and transferred to the laboratory where they were stored at room temperature (21-24°C). On December 29, 1968, these cells were opened and five were found to contain *Anthrax l. artemisia* (one mature larva and four adults).

The same 68 host cells also included three containing *Z. maculata* (two prepupae and one adult). Various stages of *Z. maculata* were also found in 36 additional cells excavated in 1968. The biology agreed with that reported by Torchio and Youssef (1968), but additional details of its ethology were observed. (1) In one cell, an egg chorion of the parasite was found attached to the cell wall immediately below the cap. A scar visible only on the inner face of this cap indicated that the parasite had drilled a hole through it, attached an egg to the cell wall rather than to the cap, and then repaired the cap. (2) In one cell, the first-instar parasite punctured the host egg, migrated a short distance along the surface of the provision, and then ingested a small quantity of it before molting. The head capsule below the antennae was immersed in the provision during feeding. (3) The second and subsequent instars, like those of the host, consumed the outer edge of the provision, but they periodically meandered across the surface of the provision and consumed the developing central pillar. (4) Also, territoriality was evidenced by three male *Z. maculata* which were observed perched on plants of inland salt grass [*Distichlis stricta* (Torr.) Rybd.] 6 to 9 m in front of the nesting embankment. Two were dusted with marking powder, and each was subsequently found perched on plants growing over a particular square meter surface during various periods through four consecutive days. Each time another *Z. maculata* flew over an occupied plant, the "owner" took flight and grasped the second bee, causing both to fall. Then, the "owner" immediately assumed a copulatory position and used his antennae to stroke those of the invader. Coition was not observed because every invader proved to be a male. When pebbles approaching the size of an adult *Z. maculata* were tossed near a perched male, he flew up, examined the intruding object, and returned to his perch.

A fungus, *Ascosphaera apis* (Maassen ex Claussen) Olive and Spiltoir, was found in most cells of *Anthophora peritomae*, and hyphae were visible on feces of the host bees within 24 hours after defecation was completed. Forty-eight hours later, a solid mat of mycelia and nutriocytes covered the feces. Some fecal particles were embedded in this mycelial mat, and each particle became shrunken, collapsed, and brittle.

In Europe, *Ascosphaera apis* sometimes attacks larvae of *Apis mellifera* L. and causes an infection known as chalk brood disease (Maassen, 1916). Recently chalk brood disease has been reported from honey bee colonies in the United States.

Melville and Dade (1944) and Clout (1956) were the first to report the incidence of *Ascosphaera apis* on wild bees (*Megachile* sp. and *Chalicodoma* sp., respectively). The fungus infests the bee larva after it attacks the pollen provision, according to Clout. Baker and Torchio (1968), reported the first incidence of this fungus from the New World in cells of two species of wild bees, *Megachile* (*Megachile*) *inermis* Provancher and *Anthophora* (*Anthophora*) *pacifica pacifica* Cresson. They associated the fungus with the

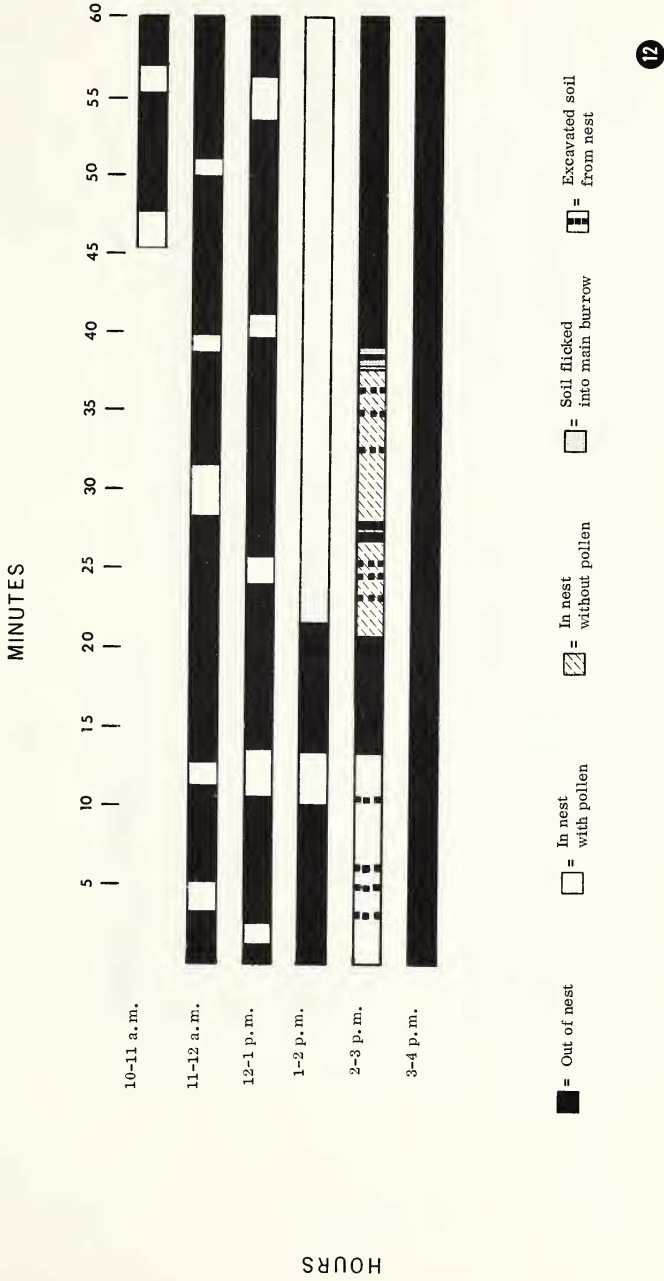
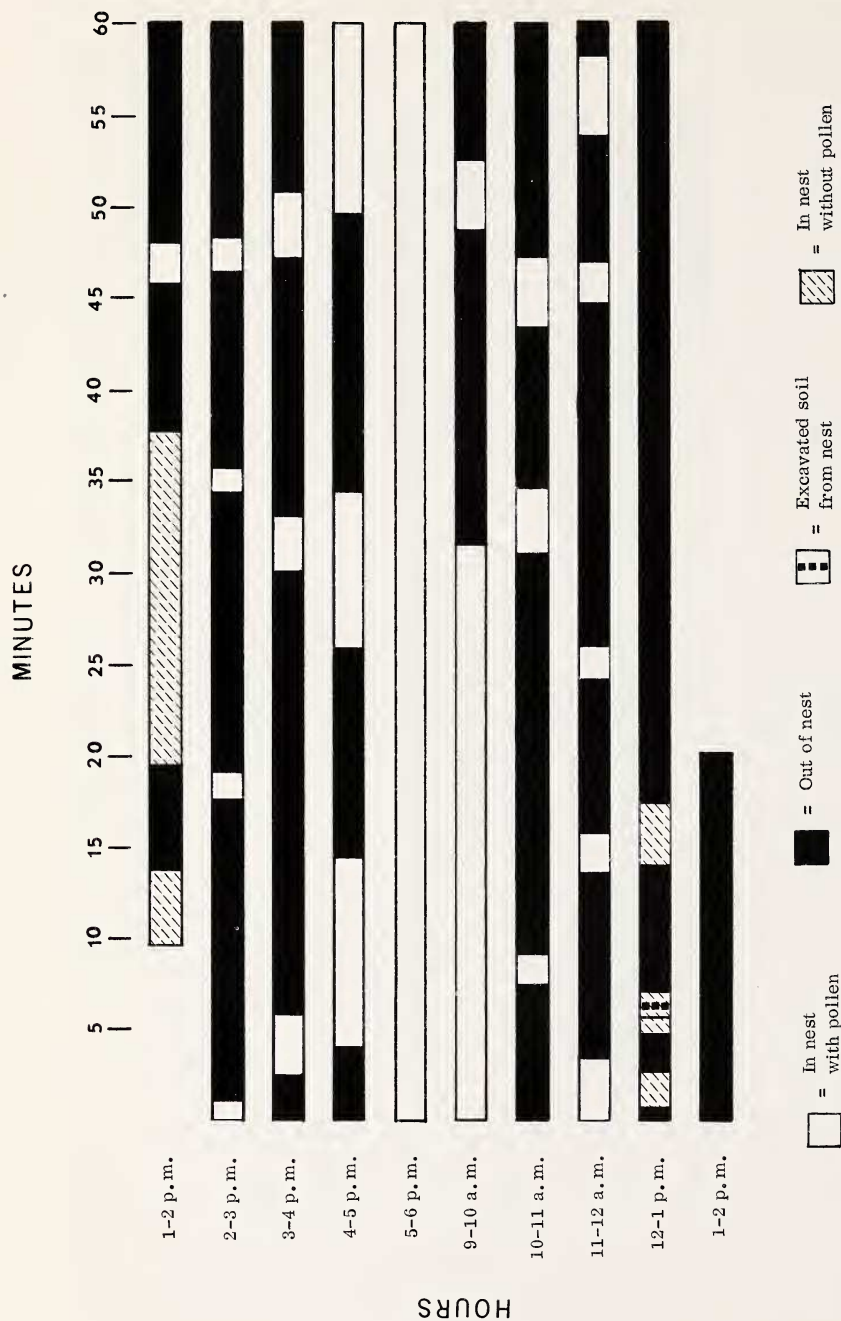


FIGURE 12. Nesting activities of *Anthophora flexipes* during cell provisioning.



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FIGURE 13. Nesting activities of *Anthophora peritomae* during cell provisioning.

feces in both species but did not recover infested larvae. In *Anthophora peritomae*, the fungus did not appear in cells parasitized by *Zacoscia* nor in cells in which the host larva died before or during defecation. Apparently, *Ascosphaera apis* in the New World does not infect the larvae of bees other than honey bees.

DISCUSSION

In Table I the contrasting features in the bionomics of *Anthophora peritomae* and *A. flexipes* are outlined. Of the 13 items, numbers 1 through 5 are probably of specific significance; the others are more likely expressions of habits imposed on the bee by the niches in which nesting occurred. Items 6 and 7, for example, may simply reflect the different host plants available to each species. *Anthophora peritomae* visited *Grindelia squarrosa*, whereas *A. flexipes* visited several hosts growing in abundance near its nest sites. Perhaps the moistness of the provision and the presence or absence of a nectar layer may be correlated with the host plants rather than with the species of bee. Apparently, *Z. maculata* survives equally well on either a solid- or liquid-surfaced provision. Numbers 8 through 13 may simply reflect a more crowded condition at the nest site of *A. peritomae*.

TABLE I

Ethological differences between *Anthophora peritomae* and *Anthophora flexipes*
(+ = yes; - = no)

	<i>A. flexipes</i>	<i>A. peritomae</i>
1. Area immediately above each cell carved into a pocket lined with small soil particles	-	+
2. Anal excreta smeared on cell wall before defecation	-	+
3. Feces deposited as a continuous, thin layer covering cell walls	+	-
4. A transparent thread traverses the central core of each fecal particle and interconnects them	-(?)	+
5. Salivary material secreted	-	+
6. Pollen initially stored in a dry state	-	+
7. Surface of provision covered with a nectar layer	+	-
8. Initiation of nesting restricted to morning	+	-
9. Nest entrances enter substrate at a particular angle	+	-
10. Lateral burrows in each nest mostly parallel	+	-
11. Some old burrows refurbished	-	+
12. Some old cells refurbished	-	+
13. Some nests communal	-	+

A. peritomae demonstrates the following biological habits heretofore unnoticed within the genus: salivary material is secreted by the larvae; old cells are refurbished; and communal nest entrances are used. Provisioning of cells by more than one individual appears to be accidental.

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